Reciprocal chromosome painting between three laboratory rodent species

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Abstract

The laboratory mouse (*Mus musculus*, $2n = 40$), the Chinese hamster (*Cricetulus griseus*, $2n = 22$), and the golden (Syrian) hamster (*Mesocricetus auratus*, $2n = 44$) are common laboratory animals, extensively used in biomedical research. In contrast with the mouse genome, which was sequenced and well characterized, the hamster species has been set aside. We constructed a chromosome paint set for the golden hamster, which for the first time allowed us to perform multidirectional chromosome painting between the golden hamster and the mouse and between the two species of hamster. From these data we constructed a detailed comparative chromosome map of the laboratory mouse and the two hamster species. The golden hamster painting probes revealed 25 autosomal segments in the Chinese hamster and 43 in the mouse. Using the Chinese hamster probes, 23 conserved segments were found in the golden hamster karyotype. The mouse probes revealed 42 conserved autosomal segments in the golden hamster karyotype. The two largest chromosomes of the Chinese hamster (1 and 2) are homologous to seven and five chromosomes of the golden hamster, respectively. The golden hamster karyotype can be transformed into the Chinese hamster karyotype by 15 fusions and 3 fissions. Previous reconstructions of the ancestral murid karyotype

proposed diploid numbers from $2n = 52$ to $2n = 54$. By integrating the new multidirectional chromosome painting data presented here with previous comparative genomics data, we can propose that syntenies to mouse Chrs 6 and 16 were both present and to hypothesize a diploid number of $2n = 48$ for the ancestral Murinae/Cricetinae karyotype.

Introduction

Myomorph rodents, e.g., rats, mice, voles, hamsters, jerboas, and many allied forms, are a particular group of species characterized by extremely high rates of chromosome evolution and remarkable chromosome polymorphism (wide variation in diploid numbers, heterochromatin quantity, and possession of supernumerary B chromosomes) (Graphodatsky 1989; Murphy et al. 2001). This has made myomorph rodents difficult to study using comparative chromosome analysis (Scherthan et al. 1994). Cross-species chromosome painting within the myomoph group has been done only for some species of the Muridae family: *Mus musculus* and *Rattus norvegicus* (Guilly et al. 1999, 2001; Stanyon et al. 1999), *R. rattus rattus* and *R. rattus frugivorous* (Cavagna et al. 2002), *M. musculus* and *C. griseus* (Yang et al. 2000), *M. musculus* and *Apodemus sylvaticus* (Stanyon et al. 2004), *M. musculus* and *Mus platythrix* (Matsubara et al. 2003), *M. musculus* and *Otomys irroratus* (Engelbrecht et al. 2006), *M. musculus* and *Rhabdo-*

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mys pumilio (Rambau and Robinson 2003), and *M. musculus* and seven species of *Apodemus* (Matsubara et al. 2004). Homologies between some chromosomes of *M. musculus* and *Peromyscus maniculatus* were partly defined (Dawson et al. 1999).

In earlier comparative studies of chromosome G-banding patterns, some homologous elements in the mouse and the Chinese hamster karyotypes were found (Gamperl et al. 1978; Graphodatsky 1989). However, no genome-wide comparison of these two karyotypes was possible until reciprocal painting between rodent species from Cricetinae (Chinese hamster) and Murinae (mouse) subfamilies confirmed intensive chromosome rearrangements during their karyotype evolution (Yang et al. 2000). No data have been reported so far on chromosome painting of the golden hamster.

In this article we present a chromosome comparison of the laboratory mouse (*Mus musculus*, $2n = 40$), the golden hamster (*Mesocricetus auratus*, $2n = 44$), and the Chinese hamster (*Cricetulus griseus*, $2n = 22$) using three sets of painting probes. Here golden hamster painting probes were used for the first time to compare karyotypes of these rodents in detail. We performed the reciprocal painting between the Chinese hamster and golden hamster and between the mouse and golden hamster karyotypes.

Materials and methods

Animals. Chromosome suspensions were obtained from a fibroblast cell line in the Laboratory of Human and Animals Cytogenetics, the Institute of Cytology and Genetics, Russia, and in the Museum National d'Histoire Naturelle, Origine, Structure et Evolution de la Biodiversite, Paris, France.

Cell culture and metaphase preparation. Fibroblast cultures were established from male specimens of mouse, Chinese hamster, and golden hamster. Cells were cultivated in alpha-DMEM supplemented with 10% fetal bovine serum. Metaphase chromosome spreads were prepared from primary fibroblast cultures as described previously (Yang et al. 1999, Graphodatsky et al. 2000, 2001).

Nomenclature of golden hamster chromosomes. The golden hamster (*M. auratus*) karyotype was reported earlier but no standard nomenclature of chromosomes has been proposed (Popescu and DiPaolo 1972; Pavia et al. 1977; Li et al. 1982; http://www.bionet.nsc.ru). The diploid chromosome number ($2n = 44$) and fundamental number found in

this study were the same as those reported previously. The chromosomes are numbered according to Radjabli et al. (2006).

Painting probes. We used painting probes derived from the mouse and the Chinese and golden hamsters to perform cross-species chromosome painting. The sets of mouse (Yang et al. 2000; Stanyon et al. 2004) and Chinese hamster (Yang et al. 2000) paints reported previously were used in this study. Briefly, this set of Chinese hamster painting probes consisted of nine probes, each representing one chromosome, and one probe containing both autosomes 9 and 10. Both sets of laboratory mouse painting probes consisted of 20 probes and represented all individual autosomes and the X chromosome. Hybridizing the probes onto G-banded chromosomes of the same species identified the content of each paint.

The golden hamster paints were generated in the Key Laboratory of Cellular and Molecular Evolution, Chinese Academy of Sciences, by degenerative oligonucleotide priming (DOP)-PCR amplification of flow-sorted chromosomes (Telenius et al. 1992; Yang et al. 1995) with the exception of the painting probes for Chromosomes 15, 16, and 21 of golden hamster, which were obtained by microdissection as described (Trifonov et al. 2002).

Fish. G-banding was performed before fluorescence *in situ* hybridization (FISH), using the standard procedure (Seabright 1971). Metaphases were photographed, slides destained in methanol, and fixed with 1% formaldehyde. FISH was performed using a standard protocol (Yang et al. 1999, Graphodatsky et al. 2000). In short, for each hybridization experiment we used 0.2 μg biotinylated DOP-PCR product and 30 μg Cot-5 DNA of *M. auratus* in 15 μl of hybridization buffer (10% dextran sulfate, 50% formamide, 2×SSC). Paints were denatured at 96°C for 3 min and reannealed for 30 min at 42°C. Probes were hybridized overnight at 42°C. Posthybridization washes included 40% formamide, 2×SSC 3 times, 2×SSC 3 times (5 min each), followed by 30-min incubation in 3% dry milk in 4×SSC/0.1% Triton X-100. All washes were performed at 42°C. Hybridization signals were detected with avidin-FITC without further amplification. Chromosomes were counterstained with DAPI.

Image capture. Images were captured using In Situ Imaging System (ISIS) software (Metasystems) with a Paco CCD camera mounted on an Aristoplan (Leitz) microscope. The microscope was equipped with two filter sets for FITC and DAPI, respectively.
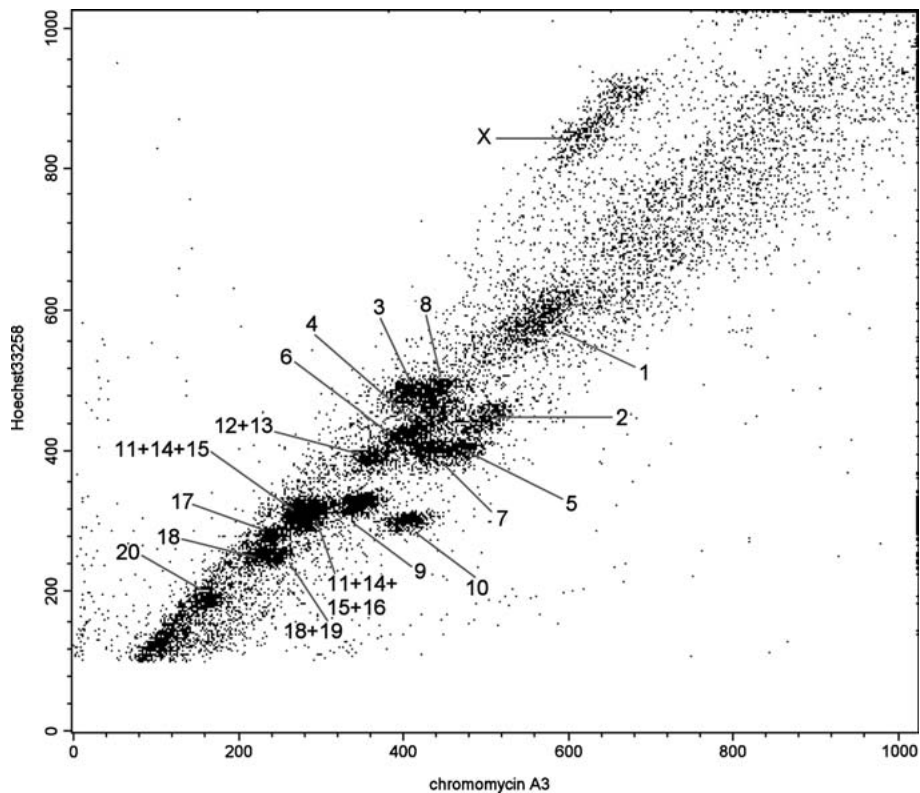
Fig. 1. Bivariate flow karyotype of the golden hamster cell line with chromosomal assignments.

Fluorescence signals were captured separately as 8-bit black-and-white images through appropriate excitation filters, normalized, and merged to a 24-bit color image. Hybridization signals were assigned to specific chromosome regions defined by G-banding patterns previously photographed and captured by the CCD camera. All image processing was performed using Paint Shop Pro (Jasc Software).

Results

Golden hamster flow karyotype. The set of golden hamster (*M. auratus*, 2*n* = 44) chromosomes was separated into 17 regions (Fig. 1). As the karyotype of the golden hamster contains many metacentric chromosomes with similar size and base ratio, it was difficult to resolve some individual chromosomes by sorting. The content of each peak was identified by hybridizing the probes onto G-banded chromosomes of the golden hamster. Eleven peaks each contained a particular chromosome (1, 2, 3, 5, 7, 8, 9, 10, 17, 18, and 20); four peaks provided hybridization signals on two chromosomes (X and Y, 4 and 6, 12 and 13, 18 and 19), while two probes highlighted three and four chromosomes (11, 14, 15 and 11, 14−16). To refine the resolution of analysis, microdissection of some golden hamster chromosomes (15, 16, and 21) was performed. Thus, 20 painting probes, containing all 19 golden hamster autosomes and the X chromosome,

were used in this study: 1, 2, 3, 4+6, 5, 7, 8, 9, 10, 11+14+15, 11+14+15+16, 12 +13, 15, 16, 17, 18, 18+19, 20, 21, and X.

Reciprocal chromosome painting of Chinese and golden hamsters. Examples of FISH are shown in Fig. 2a, b. The 20 painting probes of the golden hamster revealed 25 conserved autosomal segments in the genome of the Chinese hamster (Fig. 3). Almost all probes (Chrs 1−4, 6−8, 10, 12, 13, 15−21, and X) delineated one region on the Chinese hamster chromosomes. Other golden hamster probes (Chrs 5, 9, 11, 14) each delineated two regions in the *C. griseus* karyotype. The reciprocal hybridization of nine Chinese hamster painting probes produced 23 signals on golden hamster autosomes (Fig. 4). Five Chinese hamster chromosome probes (6−9 and X) painted one region on the golden hamster karyotype, three probes (Chrs 3−5) each delineated two regions on golden hamster autosomes, and two probes (Chrs 1 and 2) painted seven and five regions, respectively.

Even though there are twice as many chromosomes in the golden hamster (2*n* = 44) as in the Chinese hamster (2*n* = 22), homologous regions defined by chromosome painting showed good correspondences in their banding patterns, suggesting that there were limited intrachromosomal rearrangements. However, for some segments on Chrs 1 and 2 of the Chinese hamster, it was hard to
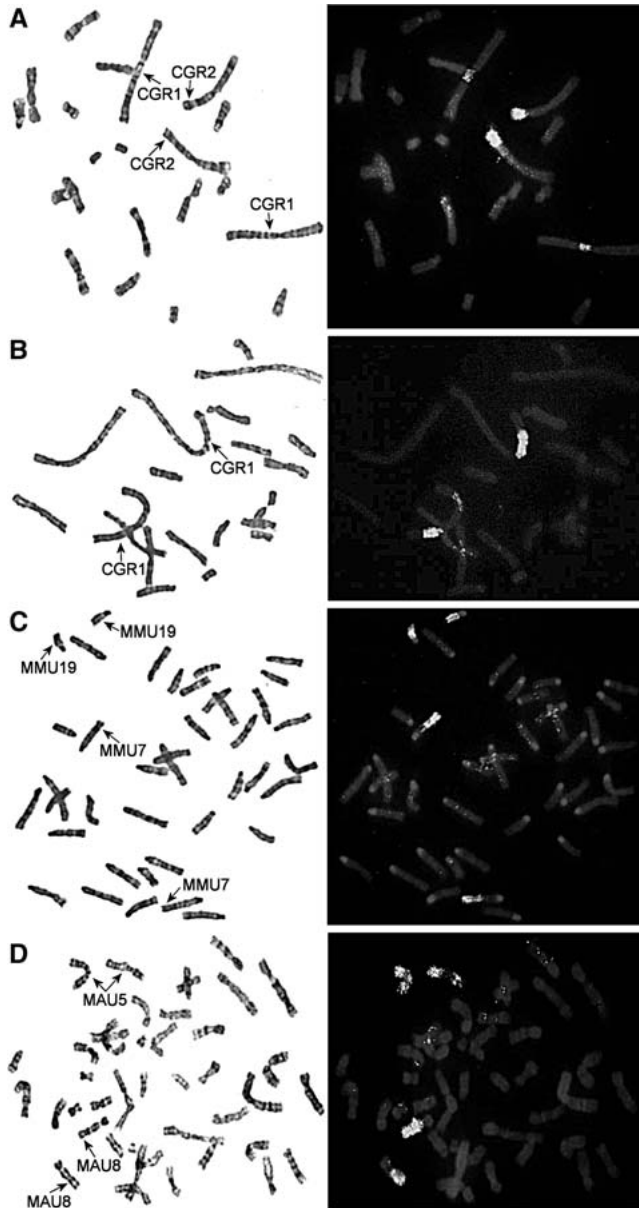
Fig. 2. Examples of fluorescent *in situ* hybridization: (**a**) localization of painting probe of Chr 5 of *M. auratus* on *C. griseus* chromosomes; (**b**) localization of painting probe of microdissected Chr 16 of *M. auratus* on *C. griseus* chromosomes; (**c**) localization of *M. auratus* Chr 2 on *M. musculus*; (**d**) localization of *M. musculus* Chr 1 on *M. auratus* chromosomes.

show homology of the banding pattern because of the small size of fragments.

The two largest chromosomes of the Chinese hamster (Chrs 1 and 2) are homologous to seven and five golden hamster chromosomes, respectively (Fig. 3). Chromosomes 5 and 14 of the golden hamster both contain the association 1 and 2 of *C. griseus* chromosome segments (Fig. 4). The golden hamster karyotype can be formed from the Chinese hamster karyotype by 13 fissions and 2 fusions,
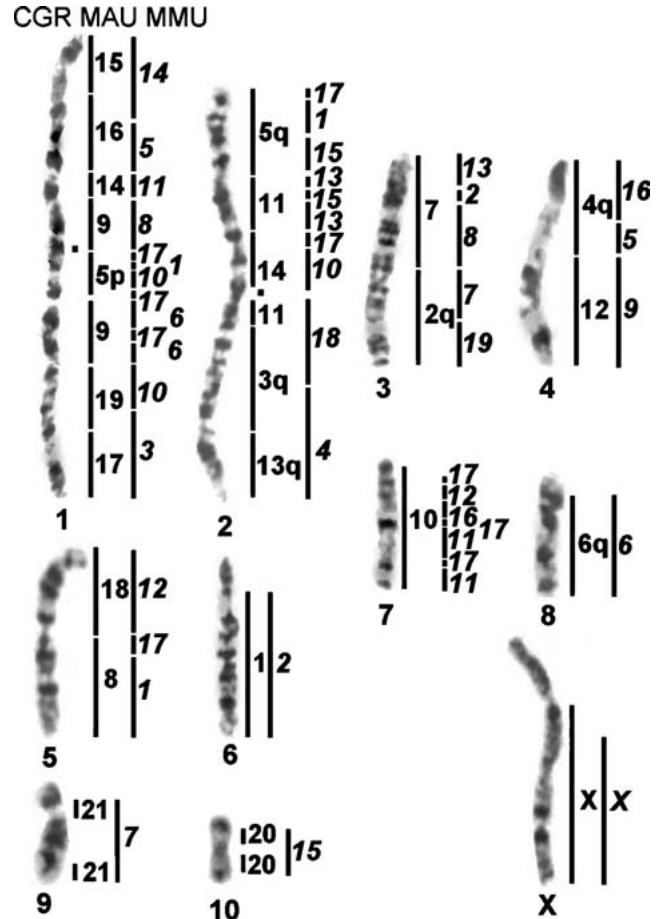

Fig. 3. Comparative chromosome map of Chinese hamster (CGR, banded chromosomes at the left) and golden hamster (MAU, black line) established by reciprocal hybridization of golden and Chinese hamster chromosome-specific painting probes. At the right is presented correspondence to mouse chromosomes (MMU, black line) established by Yang et al. (2000) and refined by reciprocal painting of mouse and golden hamster chromosome-specific painting probes.

whereas 15 fusions and 3 fissions are needed to transform the golden hamster karyotype into the Chinese hamster karyotype.

Reciprocal chromosome painting of mouse and golden hamster. The 20 painting probes of golden hamster revealed 43 conserved autosomal segments in the mouse genome (Fig. 5). The whole set of mouse chromosome-specific probes revealed 42 conserved autosomal segments in the golden hamster karyotype (Fig. 4). Examples of FISH are shown in Fig. 3c, d. Three probes (mouse Chrs 9, 19, and X) each painted one chromosomal region of *M. auratus*. Thirteen probes (mouse Chrs 2–8, 11–14, 16, and 18) each delineated two regions on the golden hamster karyotype. The mouse probes 1, 10, and 15 painted three regions while probe 17 painted 5 regions in the *M. auratus* genome.
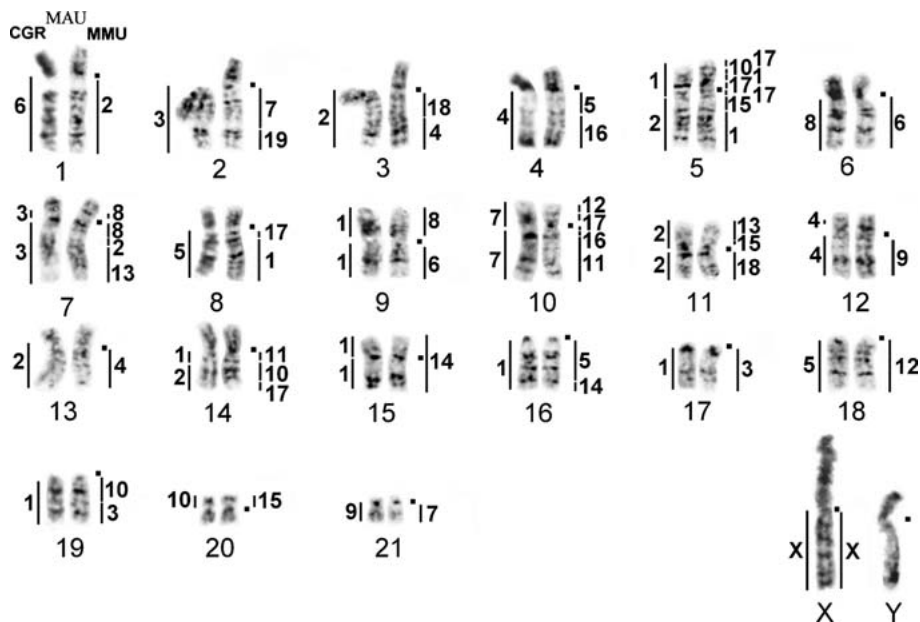
Fig. 4. G-banded karyotype of *M. auratus* (Mau, on the middle) with hybridization signals from *C. griseus* (CGR, on the left) and *M. musculus* (MMU, on the right) probes.

Reciprocal hybridization of mouse and golden hamster chromosome paints revealed the following associations of *M. auratus* chromosomal segments in *M. musculus*: 5pa/5qa/8a, 1/7a, 17/19a, 3a/13, 4a/16a, 6/9a, 2a/21, 7b/9b, 14a/5pb/19b, 10a/14b, 10b/18, 7c/11a, 15/16b, 5qb/20/11b, 4b/10c, 14c/10d/5pc/8b/10e/5qc, 3b/11c (Fig. 5). Twelve mouse chromosome associations are present in the golden hamster karyotype (Fig. 4). Mouse Chromosomes 1 and 17 painted disjunct regions on Chromosome 5 of the golden hamster with signals on both the p and q arms. The most probable explanation for this pattern is that an inversion occurred in the golden hamster karyotype.

Discussion

This article presents the first report on reciprocal painting between two species from the Cricetinae, the golden hamster and the Chinese hamster. We also used multidirectional chromosome painting to provide a more accurate and full assessment of chromosomal rearrangements and breakpoints between three laboratory rodent species (mouse, Chinese hamster, and golden hamster). These data provide new information for the reconstruction of the ancestral Murinae/Cricetinae karyotype, which may well have implications for the content of the ancestral muroidea genome.

Murinae and Cricetinae karyotypic relationships. Earlier chromosomal comparison of mouse (Murinae) and Chinese hamster (Cricetinae) by reciprocal chromosome painting was carried out and a
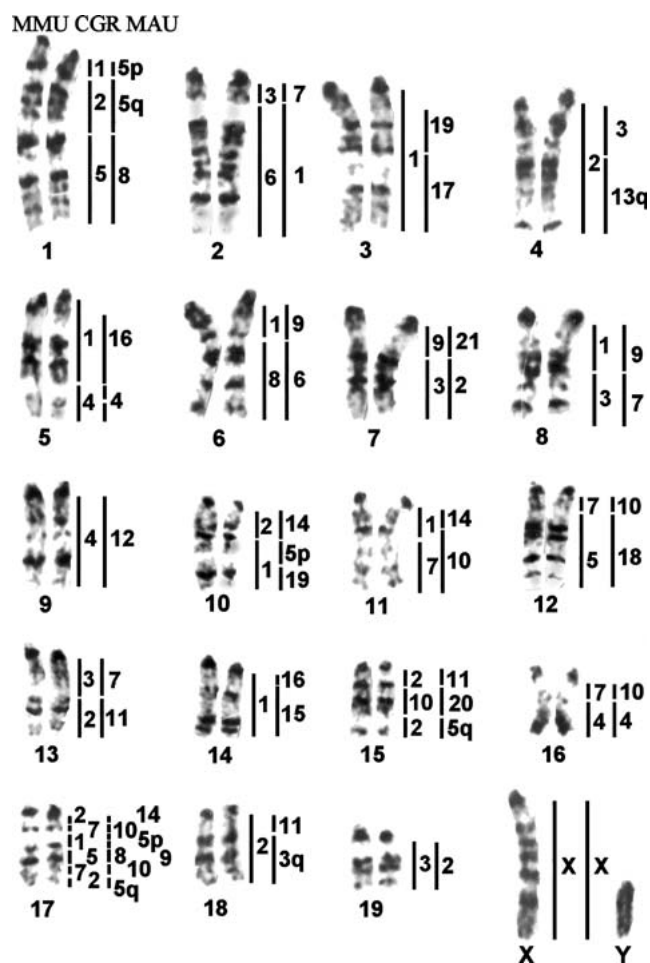

Fig. 5. The correspondence of mouse chromosomes (Mmu, on the left) and homologic segments of *C. griseus* (CGR, in the middle) by Yang et al. (2000) and *M. auratus* (MAU, on the right) established by the reciprocal painting of mouse and golden hamster chromsomes.
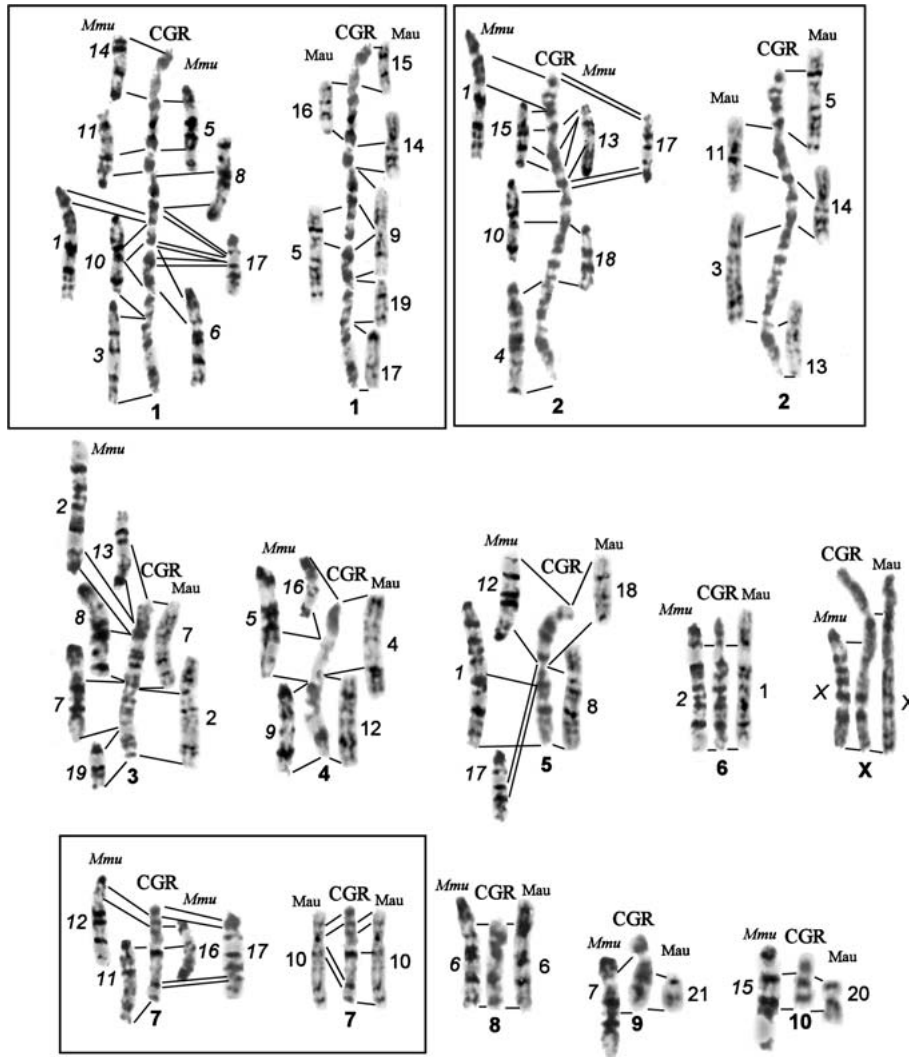
Fig. 6. G-banding comparisons of chromosomes between *M. musculus* (Mmu), *C. griseus* (Cgr), and *M. auratus* (Mau) as identified by FISH. Bold numbers mark *C. griseus* chromosomes. Chromosomes of *M. musculus* and *M. auratus* are indicated by italic and roman fonts, respectively. The correspondence of *C. griseus* Chrs 3−6, 8−10, and X (CGR, in the middle) and homologic segments of *M. musculus* (on the left) and *M. auratus* (on the right) are shown by lines. The correspondence of the most complex chromosomes of *C. griseus* (1, 2, and 7) with *M. musculus* and *M. auratus* chromosomes is shown separately within a framework.

comparative chromosome map for these two species was built (Yang et al. 2000). The use of three different sets of painting probes along with published data on these previous reciprocal data permitted us to make a more detailed chromosome comparison of *M. auratus*, *C. griseus*, and *M. musculus* and find additional intrachromosomal rearrangements distinguishing the hamsters and mouse karyotypes.

The comparative chromosome map for these three rodent species defines regions of homology between the karyotypes (Fig. 6). It is interesting that although Chromosome 7 of *C. griseus* seems to have almost the same banding pattern as Chromosome 10 of *M. auratus*, the distribution of mouse chromosome segments on these homologous chromosomes varies. This indicates possible inversion events (at least three rearrangements are necessary to convert the segment order) (Fig. 6). Clearly, apparently conserved or identical banding patterns permit hypotheses of conserved gene order, which need to be tested at the molecular level. In the case of fusion 13/15 of

mouse chromosomes on *C. griseus* Chromosome 2, we suggest that an inversion occurred in the Chinese hamster.

Chromosome 9 of the golden hamster revealed two homologous segments on Chinese hamster Chr 1. It is possible that the segments were derived by an inversion. However, because these segments are present in different mouse chromosomes (MMU6 and MMU8), one could suggest that they were present as two chromosomes in the common ancestor of hamsters and mouse. *M. auratus* Chr 11 is present on two regions of *C. griseus* Chr 2 and gives three signals in the mouse genome (MMU13, 15, and 18). The pattern of the probe distribution may indicate that MAU11 was present as two chromosomes in an ancestor Eumuroida karyotype (corresponding to MMU13/15 and MMU18).

Implication for the ancestral Eumuroida karyotype. There are 14 rodent species studied up to now using mouse painting probes (Guilly et al. 1999,
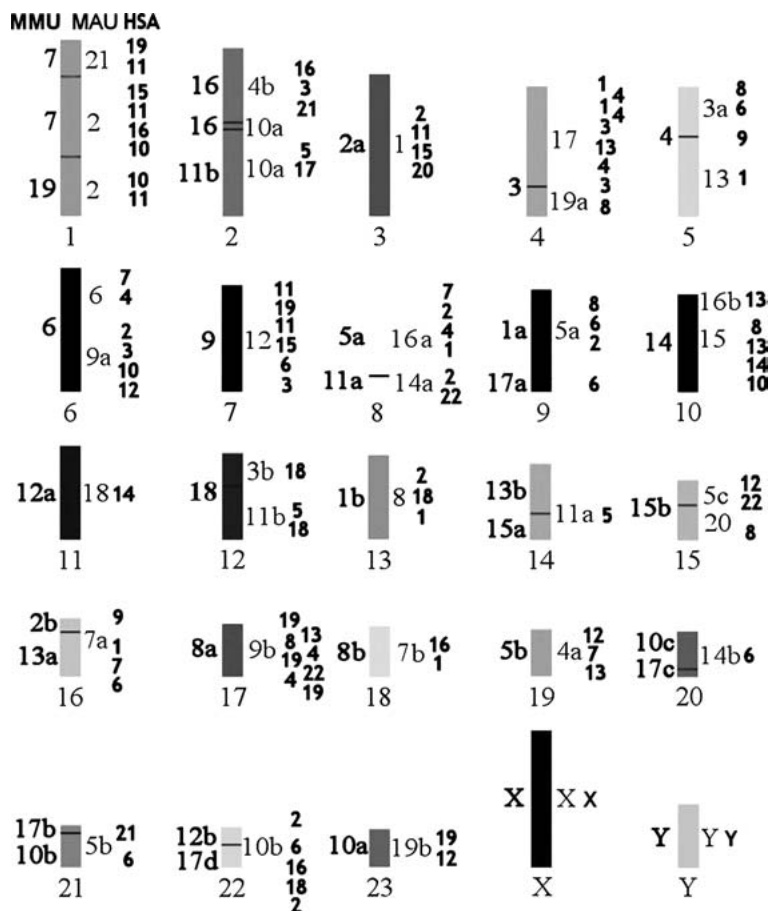
Fig. 7. Reconstructed ancestral Eumuroida karyotype. The homologies of individual conserved segments to mouse and golden hamster chromosomes are shown to the left and to the right of the ideograms, respectively. Beside each chromosome of the ancestor is shown its possible homology with conforming fragments of human chromosomes.

2001; Stanyon et al. 1999, 2004; Yang et al. 2000; Cavagna et al. 2002; Rambau and Robinson 2003; Matsubara et al. 2003; Engelbrecht et al. 2006).

All reported species belong to two subfamilies the Murinae (7 *Apodemus* species, *Otomys*, *Rhabdomys*, 2 *Rattus* species, 2 *Mus* species) and Cricetinae (*Cricetulus*) within the large superfamily Eumuroida (Steppan et al. 2004). These data allow speculation about the course of chromosome evolution in this group. The data may also have implications for some previous hypothesis concerning the ancestral Eumuroida karyotype (AEK). However, it should be noted that the current sample of taxa is still extremely thin for one of the largest mammalian clades. All conclusions can be considered working hypotheses which can help clarify future research directions. The presence of the same combination of chromosome segments in different species may indicate the ancestral origin of the syntenic group. Yang et al. (2000) suggested earlier that associations of mouse chromosomal segments 7/19 (AEK1), 13/15 (AEK14), 12/17 (AEK22), 17/1/17 (AEK9), 5/11 (AEK8), 2/13 (AEK16), and 11/17 may represent ancestral syntenies for rodents with mouse Chrs 3

(AEK4), 4 (AEK5), 9 (AEK7), 18 (AEK12), and 19 being presented as single chromosomes.

According to another hypothesis, the ancestral karyotype of eumuroid rodents had a diploid number of 2n = 54 and contained the following chromosomes (composed from homologous mouse chromosome segments): MMU 1(AEK13), 1/17 (AEK9), 2 (AEK3), 2/13 (AEK16), 3 (AEK4), 4 (AEK5), 5 (AEK 19), 5/11 (AEK 8), 6a, 6b, 7/19 (AEK1), 8a (AEK17), 8b (AEK18), 9 (AEK7), 10a (AEK23), 10b/17b (AEK21), 10c/17c (AEK20), 11, 11/16, 12a (AEK11), 12b/17d (AEK22), 13b/15a (AEK14), 14 (AEK10), 15b (AEK15), 16b, 18 (AEK12), X, and Y (Stanyon et al. 2004). The hypothesis was based on the comparative analysis of *M. musculus* painting data on five Murinae and one Criceninae species. Our ancestral karyotype differs in the composition of two chromosomes: AEK 2 (16/11b) and AEK 6 (Fig. 7).

A more precise structure of the ancestral Eumuroida karyotype can be defined if a species from another order is used as an outgroup. In the present study the use of the human karyotype seemed convenient. The high level of fragmentation and repatterning of the mouse genome probably accounts for the limited

Table 1. Conservation of the putative ancestral chromosomes in genomes of various rodents and human

Ancestral chromosomes	Mouse chromosome associations (Yang et al. 2000; this paper)	Golden hamster chromosome associations (this paper)	Cricetulus griseus (Yang et al. 2000; this paper)	Rattus norvegicus (Stanyon et al. 1999; Guilly et al. 2001)	Rhabdomys pumilio (Rambau & Robinson 2003)	Apodemus sylvaticus (Matsubara et al. 2004; Stanyon et al. 2004)	Otomys irroratus (Engelbrecht et al. 2006)	Mus platythrix (Matsubara et al. 2003)	Peromyscus eremicus (our unpublished data)	Microtus oeconomus (our unpublished data)	Calomyscus sp. (our unpublished data)	Homo sapiens (Murphy et al. 2005)
1	7/19	21/2	+	+	+	+	+	+	+	+	+	+
2	16/11b	4b/10a	-	+	+	+	+	+	+	+	+	+
3	2a	1	+	+	+	+	+	+	-	-	+	-
4	3	17/19a	+	+	+	+	+	+	+	+	+	-
5	4	3a/13	+	+	+	+	+	+	+	-	+	-
6	6	6/9a	-	-	+	+	+	-	+	+	+	-
7	9	12	+	+	-	+	-	+	+	+	+	-
8	5a/11a	16a/14a	+	+	-	+	-	-	-	+	-	+
9	1a/17a	5a	+	+	+	+	+	-	+	+	+	+
10	14	16b/15	+	-	+	+	+	+	-	-	-	-
11	12a	18	+	+	+	+	+	+	+	+	+	+
12	18	3b/11b	+	+	+	+	+	+	+	+	+	-
13	1b	8	+	+	-	+	-	+	+	+	-	+
14	13b/15a	11a	+	+	+	+	+	+	+	+	+	+
15	15b	5c/20	-	+	+	+	-	+	+	+	-	-
16	2b/13a	7a	+	+	+	-	+	-	-	+	+	-
17	8a	9b	+	+	+	+	+	+	+	+	+	-
18	8b	7b	+	+	+	+	+	+	+	+	+	-
19	5b	4a	+	-	+	-	-	+	+	+	+	-
20	10c/17c	14b	+	+	+	+	+	+	+	+	+	+
21	17b/10b	5b	+	+	+	+	+	-	+	+	+	+
22	12b/17d	10b	+	+	+	+	-	+	+	+	+	-
23	10a	19b	+	+	+	+	+	+	+	+	+	+
X	X	X	+	+	+	+	+	+	+	+	+	+

Exact chromosomal correspondence given for mouse and golden hamster. For other species the presence of ancestral segment is indicated by "+" and the absence of segment is indicated by "-".

success of chromosome reciprocal painting between human and mouse (Ferguson-Smith 1997). However, gene mapping and sequencing data are now available to compare the highly rearranged genomes of muroid rodents with the human genome. Using the data in Murphy et al. (2005), more then 60 mouse chromosome associations were defined for the human karyotype. Genome browsers provide even more detailed comparative maps between the human and mouse genomes and probably a higher number of associations could be described, far beyond the resolution provided by cytogenetics. For example, see mouse−human orthology map with the 113 human homologous segments mapped onto 20 *Mus musculus* chromosomes (http://www.informatics.jax.org/reports/homologymap/mouse_human. shtml).

The addition of a new hamster species (*Mesocricetus auratus*, Cricetinae) together with human and mouse genome comparisons and some of our unpublished results allowed us to test the previously suggested ancestral karyotypes (Yang et al. 2000; Stanyon et al. 2004; Engelbrecht et al. 2006) and to propose for discussion the new hypothetical Eumuroida ancestor karyotype with $2n = 48$ (Fig. 7). As the basis for construction of this karyotype, analysis of the presence or absence of chromosomal associations has served in karyotypes of the Eumuroida studied until now. In addition, we have added for this analysis unpublished data on *Peromyscus*, *Calomyscus*, and *Microtus* species (Table 1).

We propose that the ancestral Eumuroida karyotype had $2n = 48$ and contained the following murine chromosomal segments and associations: 1a/17a (MAU5a), 1b (MAU8?), 2a (MAU1), 2b/13a (MAU7a), 3 (MAU17/19a), 4 (MAU3a/13), 5a/11a (MAU16a?/14a), 5b (MAU4a), 6 (MAU6/9a), 7/19 (MAU21/2), 8a (MAU9b), 8b (MAU7b), 9 (MAU12), 10a (MAU19b), 10b/17b (MAU5b), 10c/17c (MAU14b), 11b/16 (MAU4b/10a), 12a (MAU18), 12b/17d (MAU10b), 13b/15a (MAU11a), 14 (MAU15/16b?), 15b (MAU5c/20), 18 (MAU3b/11b), X, Y. Future data from more species will contribute to more reliable reconstruction of the ancestral Eumuroida karyotype, provide insights into phylogeny, and answer questions of the mode of karyotypic changes in rodents.

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